A QUANTITATIVE EXAMINATION OF TESTICULAR GROWTH IN THE WHITE–CROWNED SPARROW [1]

DONALD S. FARNER AND A. C. WILSON

Laboratories of Zoophysiology, Department of Zoology, State College of Washington, Pullman, Washington

Since the pioneer investigations of Rowan (1925, 1926) and Bissonnette (1930) on *Junco hyemalis* and *Sturnus vulgaris,* respectively, there has been accumulated an abundance of experimental evidence which indicates that artificial elongation of the daily photoperiod in winter can cause testicular growth and development in a substantial number of temperate zone species of birds. Much of the available information has been reviewed or cited by Bissonnette (1937), Wolfson (1945, 1952), Benoit (1950), Burger (1949), Hammond (1954), Aschoff (1955) and Schildmacher and Rautenberg (1953). In general these studies contain relatively little information on the actual rates of testicular development as functions of the length of the daily photoperiod, although the investigations of Burger (1948, 1953) on *S. vulgaris,* Bartholomew (1949) on *Passer domesticus,* and Winn (1950) on *J. hyemalis* are exceptions in this respect. Despite the sparsity of data on rates of testicular development the investigations of the photoperiodic stimulation of testicular growth and development have provided the basis for widely accepted theories in which the increasing vernal day-length is regarded as the primary stimulator and timer in the testicular cycle. These theories are supported by the observations that, in at least most species studied, retention at winter day-lengths results in no development or relatively slight development. Consequently an appraisal of the photoperiodic theories indicates them to be qualitatively rational and logical, at least for many temperate zone species, but deficient with respect to quantification. Because of this deficiency it is not possible to evaluate, either individually or collectively, the roles of other variables in the natural course of testicular development. It is the function of this paper to present approximate quantifications of the function of day-length in testicular development and consequently to indicate the approximate magnitude of the roles of other variables in natural testicular development in a population of the white-crowned sparrow, *Zonotrichia leucophrys gambelii.* The analyses to be presented here suggest arguments against the objections of Blanchard (1941) and Marshall (1952, 1955) to the photoperiodic theories. The data on which our analyses are based were obtained in the course of an extensive series of experiments on the mechanism of photostimulation of testicular development.

MATERIALS AND METHODS

Our experimental birds were captured with Japanese mist nets from a wintering population in the Snake River Canyon in southeastern Washington (Mewaldt and

Farner, 1953). Prior to the beginning of the experiments they were held in large outdoor aviaries. For experimental lighting they were placed, one or two per cage in small cages ($8\frac{1}{2} \times 10 \times 16$ inches), or three or four per cage in larger cages ($12 \times 24 \times 18$ inches). Illumination was provided with incandescent lamps at an intensity of 40–60 foot candles which is substantially above the maximal intensity (*i.e.*, minimum intensity at which maximum rate of development occurs) of about four foot candles. The birds were fed a vitamin- and mineral-enriched chick-starter mash prepared according to a formula developed by the Department of Poultry Science of the State College of Washington. Food and water were available at all times. Except as otherwise noted the experimental birds were held at 20–24° C.

Immediately after removal, testes were placed in acetic acid-formaldehyde-ethanol fixing mixture. After five days they were transferred to 70% ethanol and five days thereafter weighed with a Roller-Smith torsion balance.

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TESTICULAR WEIGHT AS A FUNCTION OF TIME WITH A CONSTANT DAILY PHOTOPERIOD

An examination of the weights of the testes taken at intervals during a period of treatment with constant daily photoperiods of stimulatory duration suggests a relationship which approximates a logarithmic growth curve until the combined testicular weights reach about 200 mg. If this is a good approximation then the relationship between time and testicular weight may be expressed as

$$\log_{10} W_t = \log_{10} W_o + kt, \tag{1}$$

where W_o is the initial testicular weight in milligrams, W_t is the weight at t days, and t is the period of treatment in days. As an illustration and test of this relationship, data from three experiments have been combined in Figures 1 (first-year birds) and 2 (adults). These three experiments involved treatments with 15-hour daily photoperiods at 0° C. mean temperature, 20-hour photoperiods at 20° C., and 15-hour photoperiods at 22° C., respectively. Since the rate constants (k), with t expressed in days, are different, t in Figures 1 and 2 is expressed in arbitrary relative units (1 = time required to attain 100 mg. combined testicular weight). On this basis there were no apparent differences among the three groups; therefore, they are not differentiated in Figures 1 and 2. An inspection of Figure 1 indicates that, for first-year birds, there is a reasonably good linear relationship between the logarithms of testicular weight and time up to about 200 mg. ($\log_{10} = 2.3$) and hence a reasonably good conformance with equation (1). For adults (Fig. 2) it appears possible that a weak S-relationship may exist between t and $\log W_t$. However, for purposes of comparison of rates of development among experimental groups, it appears that no useful purpose can be effected in seeking
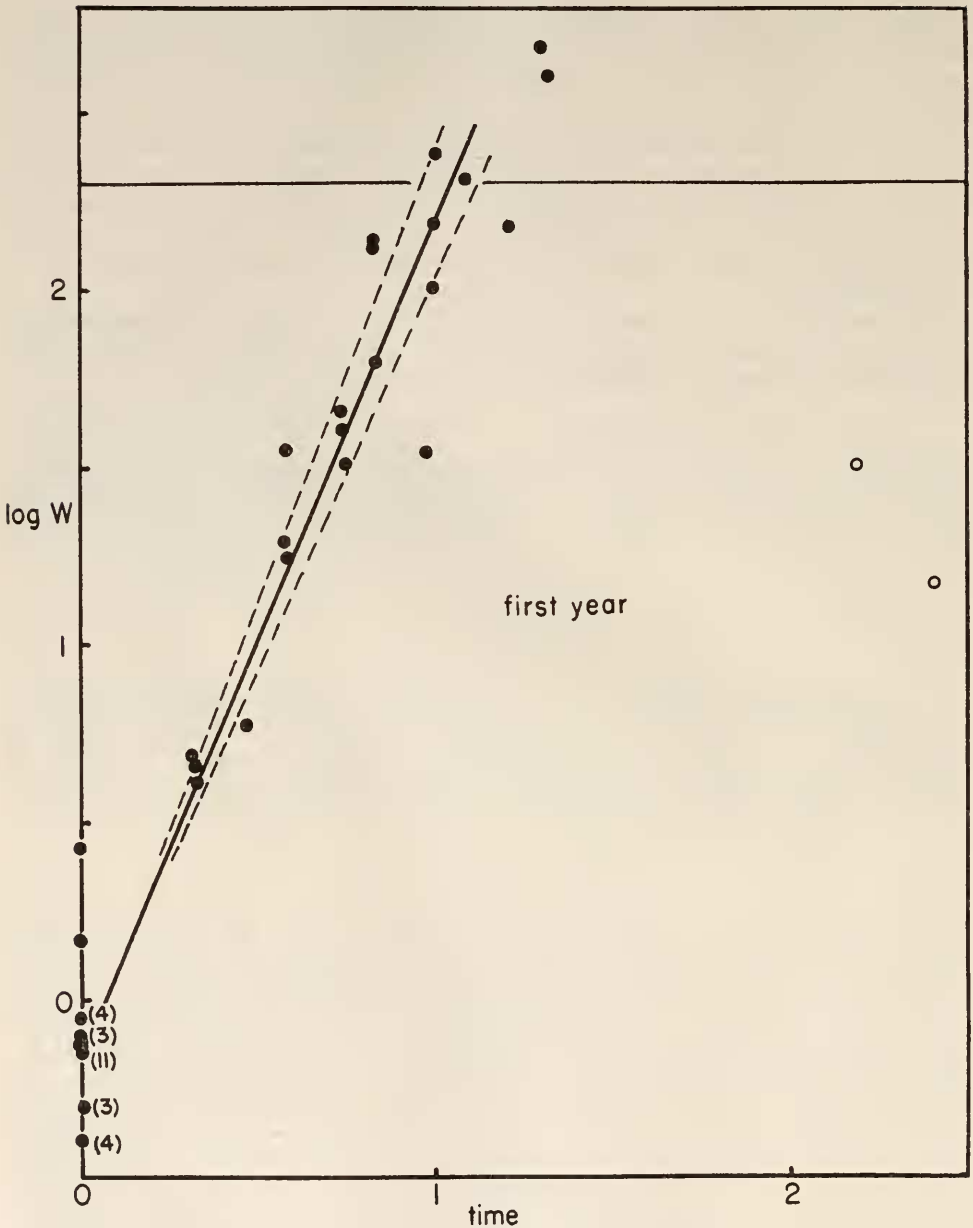
FIGURE 1. Combined testicular weights (W) of first-year white-crowned sparrows as a function of time with constant daily photoperiods of stimulatory duration. Time in arbitrary units (see text). Closed circles represent developing testes; open circles represent regressing testes. Broken lines represent upper and lower 95%-fiducial limits of the slope.

FIGURE 2. Combined testicular weights (W) of adult white-crowned sparrows as a function of time with constant daily photoperiods of stimulatory duration. Time in arbitrary units (see text). Closed circles represent developing testes; open circles represent regressing testes. Broken lines represent upper and lower 95%-fiducial limits of the slope.
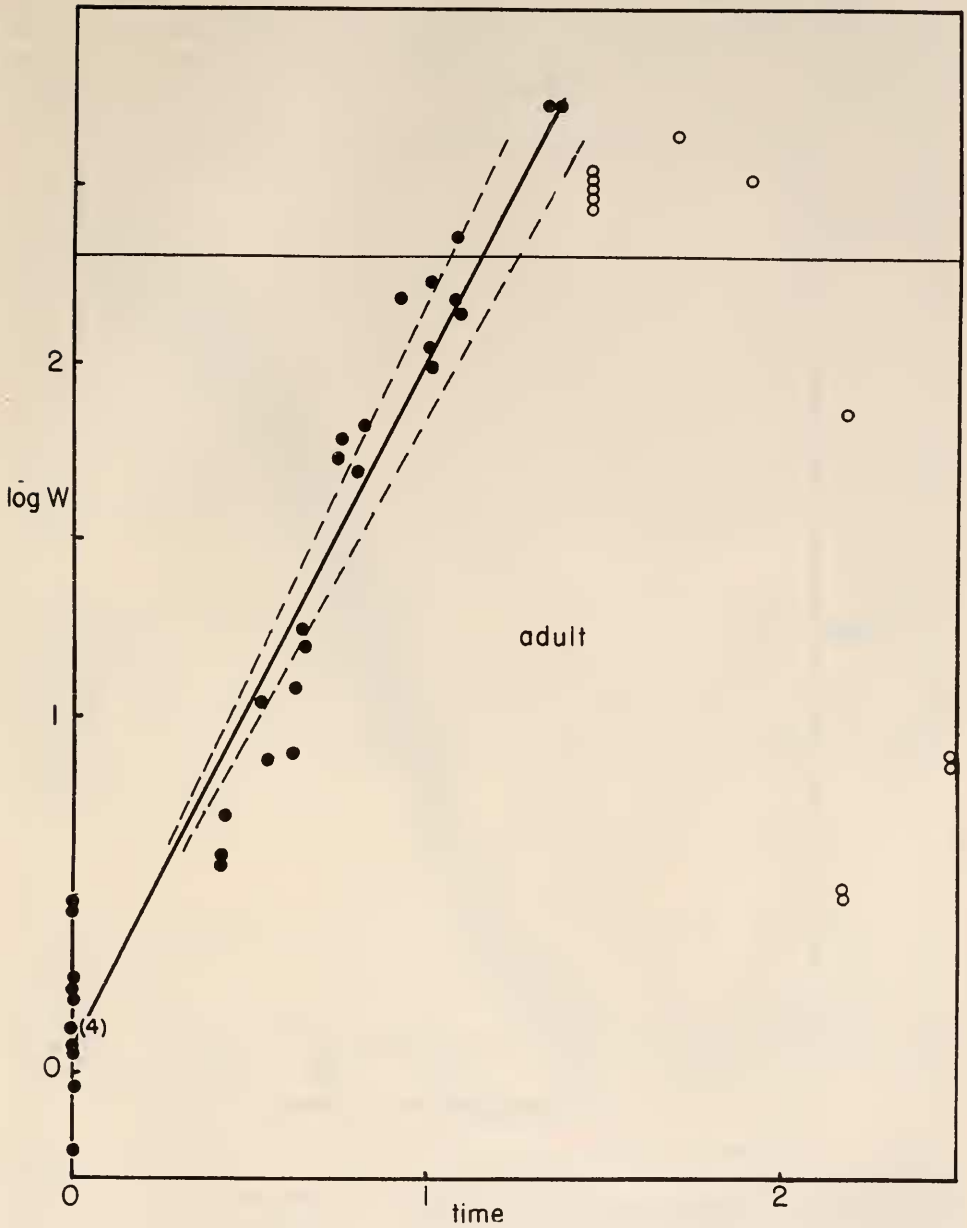
a more precise relationship.   Because of the less precise relationship between t and W_t for adult birds, it is now our policy to perform all critical experiments with first-year birds.   The solid lines in Figure 1 and 2 are drawn according to the values of k obtained by the procedure outlined by Mood (1950, Chapter 13) ; similarly
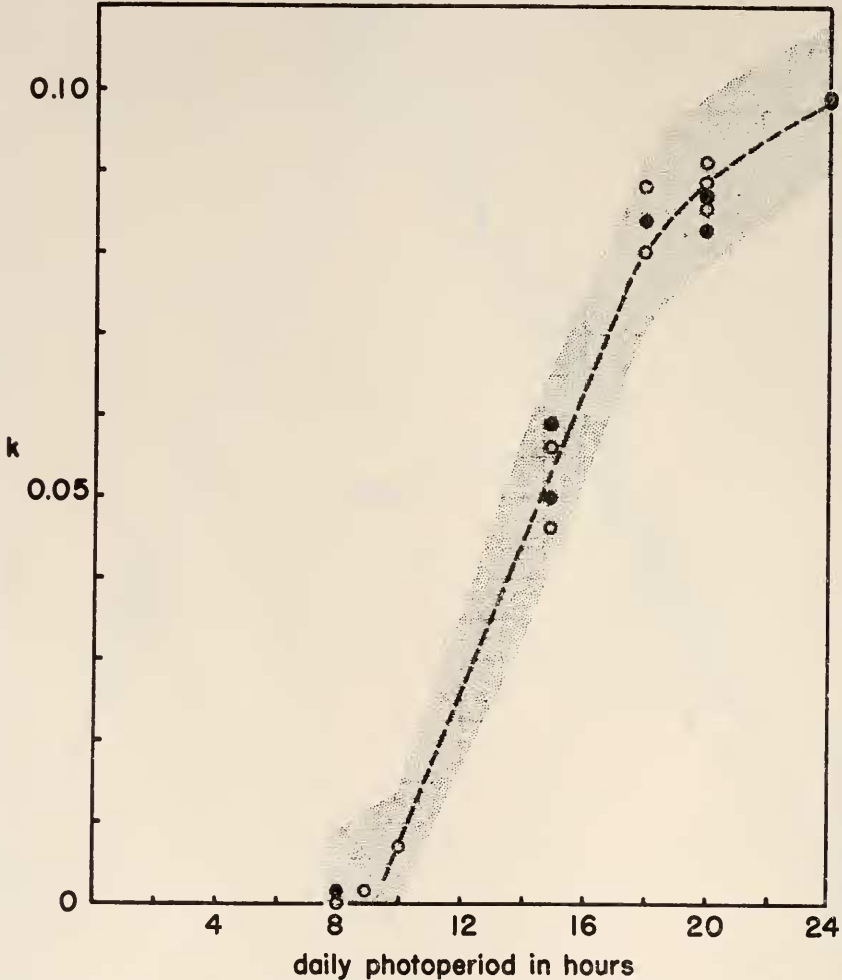

FIGURE 3. The rate of testicular development as a function of the duration of the daily photoperiod (p). See text for definition of rate constant (k). The shaded area encloses the upper and lower 95%-fiducial for all points. Open circles represent samples of first-year birds ; closed circles represent adjusted means for samples of adults.

the broken lines represent the upper and lower 95% fiducial limits, also obtained according to Mood.   In order to minimize the effect of possible non-linear relationships between log W_t and t it is now a practice in our laboratory to kill birds when the testes have attained a combined weight of about 100 mg.

The Testicular Growth Rate Constant (K) as a Function of the Length of the Constant Daily Photoperiod

An examination of k as a function of the length of a constant daily photoperiod (p) has been effected by analysis of 18 series of data (11 first-year and 7 adult) for photoperiods varying in length from 8 to 24 hours. For each of these an estimation of k and the approximate 95% fiducial limits for k were obtained according to Mood (1950). These are given in Figure 3. In the calculation of the 95% fiducial limits for k the same W_o sample was used for all groups with the same W_o date; the fiducial limits thus obtained are therefore to be regarded as estimated limits rather than true fiducial limits. As indicated above, k is greater for first-year birds than for adults, approximately 1.16 times as great for the series of data used here. Therefore in plotting the data in Figure 3, the adult values, both for estimates of k and the approximate fiducial limits, were multiplied by 1.16. The broken line, suggesting a functional relationship between p and k, has been drawn by inspection. The shaded zone on either side encloses all of the estimated fiducial limits for the individual estimates of k. It must be emphasized that this shaded zone does not represent the fiducial limits for the slope of the curve. The linear portion of the curve (between 10 and 18 hours) may be represented by

$$k_{\text{1st-yr.}} = 0.009(p - 9.1). \tag{2}$$

Obviously there is an uncertainty in the nature of the functional relationship between p and k for values of p less than 10 hours. The relatively small changes in W with respect to the natural variability of W and the errors in measurement involved with small values of W make this a difficult problem. Fortunately, as it will become evident subsequently, the values of k in this range are sufficiently small so that the calculations based on equation (2) are not serious even when it is extrapolated linearly to $k = 0$.

The Role of Environmental Temperature in the Rate of Testicular Development

For *Z. l. gambelii* it has been demonstrated earlier (Farner and Mewaldt, 1952, 1953) that the rate of testicular development with a fixed daily photoperiod of stimulatory duration is a function of environmental temperature between 0° and 22° C. It should be emphasized, however, that elevation of environmental temperature has no effect when the photoperiod is below stimulatory level (Farner and Mewaldt, 1953). Assuming, for purposes of estimation, that the effect of temperature is linear with respect to k, the following relationship should hold:

$$k_B/k_A = 1 + c(T_B - T_A). \tag{3}$$

We have estimated the value of c on the basis of two groups of birds subjected to 15-hour daily photoperiods, one at a mean environmental temperature of 1° C., the other at 22° C. On the basis of mean values of k for these two groups, c has a value of about 0.009 degrees^{-1}. Substitution of this value for c in equation (3) indicates that the role of temperature must be relatively minor. It must be observed here, however, that the responses of the lower temperature group were sufficiently variable so that, were the true k near the lower 95% fiducial limit, the

value of c would be approximately 0.019. Engels and Jenner (1956) have examined the effect of environmental temperature on the rate of testicular development in *J. hyemalis* subjected to daily photoperiods of 10–12 hours. Although differences in methods and analyses do not allow a direct comparison, it appears that c for this species must be of the order of 0.02–0.03. Similarly, from the data
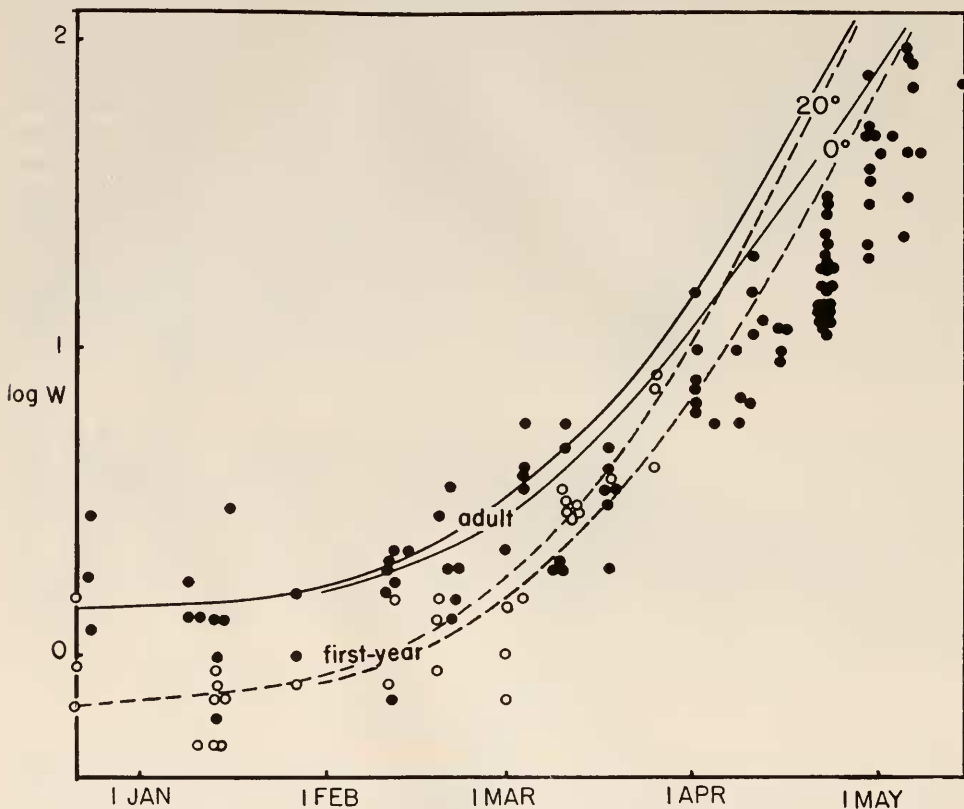

FIGURE 4. A comparison of predicted curves of testicular development with natural development. Open circles represent combined testicular weights for first-year birds taken from the Snake River Canyon population; closed circles represent combined testicular weights for adults from the same population. These groups cannot be distinguished after the prenuptial molt which occurs in late March and early April. The four curves were calculated according to equation (4) including the adjustment for temperature effects indicated in equation (3).

of Burger (1948) for *S. vulgaris* we have estimated c to be about 0.02. For these three species, then, it appears that the role of environmental temperature in testicular development is of a small, although similar, order of magnitude.

A PREDICTED COURSE OF TESTICULAR DEVELOPMENT UNDER NATURAL CONDITIONS
CALCULATED ON THE BASIS OF LABORATORY–ESTABLISHED RATES

Using the empirical relationships presented above, an attempt has been made to "predict" the course of vernal testicular development. Since environmental

temperature is an irregularly fluctuating variable, two temperature values, 0° C. and 20° C., were used for the construction of two predicted curves. For the most part the environmental temperatures fall within these limits although some sub-zero nights occur in January and February. The four curves in Figure 4 are based on values of k from Figure 3 assuming that k is a continuous positive function of p between the limits of 0 and 24 hours, k being insignificantly (< 0.002) small for all values of p below 9.1 hours. Calculations were begun with 21 December (day-length about 8.8 hours) when the mean logarithms of the testicular weights for adults and first-year birds were $+ 0.15 \pm 0.10$ and $- 0.17 \pm 0.16$, respectively. As p increases, the correspondingly larger values of k were employed; the operation may be represented by

$$\log_{10} W_n = \log_{10} W_o + \sum_{i=1}^{n} k_i, \tag{4}$$

where n is the number of days after the initial date in the calculation.

If the relationship between p and k assumed here is correct, then the day-lengths following the termination of the refractory period in mid-November (Farner and Mewaldt, 1955) would be stimulatory. Accordingly the curves in Figure 3 have been extrapolated back into November. This extrapolation indicates weights for early November which are within the range of one standard deviation of December weights and well within the range of early November weights.

An alternative interpretation of the functional relationship between p and k is that expressed by equation (2). Four curves (adults at 0° C. and 20° C., first-year birds at 0° C. and 20° C.) were therefore constructed using the equation

$$\log_{10} W_n = \log_{10} W_o + n\bar{k}_{1\ldots n} \tag{5}$$

in which,

$$\bar{k} = 0.009 \frac{\left(\sum_{i=1}^{n} p_i\right)}{n} - 0.082. \tag{6}$$

The curves obtained thus were not detectably different from those obtained by the operation noted in equation (4) and plotted in Figure 4. In the use of equations (4), (5), and (6), p has been assigned the value of the time between sunrise and sunset. Obviously this is arbitrary because of fluctuations in *effective day-length* as a consequence of differences in meteorologic conditions. That such fluctuations may affect the rate of development is obvious from our unpublished data on k as a function of light intensity. These indicate that the maximal intensity is about four foot candles whereas the minimal intensity, if such exists, is somewhat less than one foot candle. There is the additional variable of the amount of cover about the bird early in the morning and late in the evening. Our measurements of light intensities in the Snake River Canyon suggest that the period between sunrise and sunset is about as satisfactory an approximation as we can select. A discussion of the approximate magnitude of error which could be attributable to this selection of values for p is included subsequently.

A Comparison of the Actual and Predicted Curves of Vernal Testicular Development

A comparison of the predicted and natural courses of vernal testicular development is effected in Figure 4 by plotting testicular weights of birds taken in the Snake River Canyon up to the time of migration during the springs of 1952, 1953, 1955, and 1956. These data indicate that the calculations based on laboratory-established rates predict the attainment of 100-mg. testicular weights about 10 days prior to the actual time of attainment in nature. This relatively close conformance is consistent with the hypothesis that the increasing vernal photoperiod is the primary timer in the annual development of the testicular cycle. However, it is of importance to examine the possible bases for this relatively small discrepancy between the calculated and actual curves. The possible bases are both statistical and natural.

(1) *The statistical factors.* A readily apparent possible cause of the differences between the calculated and actual curves in Figure 4 is the statistical nature of the initial testicular weights employed in the calculations, 0.7 mg. for first-year birds and 1.4 mg. for adults. These are mean values for birds taken in the field during the appropriate period. The logarithms are -0.17 ± 0.16 and $+0.15 \pm 0.19$, respectively. An inspection of Figure 4 indicates that a good conformance would have occurred had the selected initial weights been about one standard deviation below the estimated means. Also important is the possible error in weighing small testes since the balance and method used in weighing have a combined error of ± 0.1 mg.

Another possible factor is the statistical nature of the slope of the line relating k as a function of p. The curve in Figure 3 has been drawn by inspection with attention both to the means and their approximate 95% fiducial limits. It can be noted that a reasonable conformance between the predicted curve and the natural data would require the slope constant a in Figure 3 and equation (2) to be 0.007 instead of 0.009. Since this appears somewhat improbable, an error in a, although possibly contributory, cannot be regarded as the primary cause of the difference. It is also possible that the functional relationship between W and t with constant daily photoperiods may differ further from the relationship in equation (1) than our data suggest. An examination of models indicates that it is very unlikely that this could be the primary source of the difference. Obviously it could be contributory.

A further possible source of error is in the value of the minimal stimulatory day-length (q), or in our assumptions concerning the relationship of k to p and the value of p where k becomes insignificantly small. However, as noted above, since very small values of k are involved such errors affect the calculated curve only slightly.

There is also the possibility of error with respect to the effect of environmental temperature as indicated by c in equation (3). As noted previously the low-temperature group which was used in the estimation of c showed considerable variability with relatively wide fiducial limits for k. If the true k were close to the lower 95% fiducial limit, c would be about 0.019 and the 0° C. curves in Figure 4 would reach the 100-mg. level about 18 days later than the 20° curves, or about nine days later than shown in Figure 4. This would give a better, although not

a complete, conformance. In other words, the statistical nature of c is such that it could contribute to the discrepancy although it is highly unlikely that it could be the sole basis for it.

(2) *The natural factors.* A possible source of the difference between the predicted curve and the natural data, as indicated above, lies in our selection of values for the effective day-length, p. The complexity of this problem has been discussed well by Bartholomew (1949). As a test of the magnitude of this source of error, we have assumed that p for each day is 30 minutes less than the period between sunrise and sunset. This alteration is almost sufficient to make the predicted curve coincide with the natural data. However, our observations on light intensities in the Snake River Canyon indicate that this assumption is unreasonable, for only rarely would p be as much as 30 minutes less than the period from sunrise to sunset; more frequently it would be somewhat greater than this period.

TABLE I

A comparison of body weights of male white-crowned sparrows in large outdoor aviaries at Pullman with those taken from the Snake River Canyon

Period	Snake River Canyon			In cages at Pullman		
	No.	Weight, grams	Standard Deviation	No.	Weight, grams	Standard Deviation
1–15 January	37	27.8*	±1.5	43	27.1*	±2.1
16–31 January	128	28.0	±1.6	51	27.8	±1.9
1–14 February	67	27.8**	±1.4	53	26.6**	±1.5
15–28 February	38	26.9	±1.2	45	27.5	±1.6
Prenuptial molt	55	27.8	±1.5	28	28.0	±2.8

* Significantly different, P $= ca.$ 0.04.
** Significantly different, P < 0.001.

Therefore, although our definition of p may be the source of some error, it is neither of sufficient magnitude nor in the right direction to account for the difference.

The estimates of k were affected with birds which had a nutritionally adequate food constantly available. The possibility exists that a nutritional difference could be involved in the differences between the calculated and actual courses of testicular development. That this possibility warrants consideration is evident from the demonstrated reduction of production of gonadotropic hormones by mammals in nutritionally inadequate states, as summarized by Ershoff (1952). Whether periods of nutritional insufficiency occur for white-crowned sparrows in the Snake River Canyon is obviously difficult to ascertain. However, a comparison can be made between the body weights of birds retained for a month or more under outdoor conditions in large aviaries at Pullman and those of birds taken from the natural population in the Snake River Canyon. The former received the same food *ad libitum* as did the experimental birds from which our laboratory-established rates were obtained. These data are summarized in Table I; it is obvious that they in no way support a hypothesis of poorer nutritional state among the wild birds. A further argument against an effective difference in nutritional state comes

from a series of 29 males held in large outdoor aviaries at Pullman. The course of testicular development for this group shows no apparent difference from that of the natural population despite the constant availability of nutritionally adequate food. Although we cannot reject completely the possibility of an interaction between low temperature and poor nutritional state, certainly we find no evidence in our data to support it.

DISCUSSION

It is patent that the greatest of caution must be applied in any inductive extrapolation of our experience with a single population of a single species. Nevertheless it may be of some value to consider briefly some possible bases for variations among the temporal patterns in the initiation of the testicular cycles of the temperate-zone passerine species in which day-length is the primary timer. In this discussion it is assumed that the basic relationships described here for Z. l. gambelii constitute, in a general way, a typical scheme.

It then becomes desirable to consider the general form of equation (2), relating day-length (p), the minimum effective day-length (q), and the rate constant (k):

$$k = a(p - q). \tag{7}$$

For arguments presented here, days (in winter) where $p < q$ must be treated as though $p = q$ and $k = 0$. This may be unrealistic, the true situation possibly being, as suggested above, that k may be a continuous positive function of p becoming insignificantly small as p becomes somewhat smaller than q. Our data are not inconsistent with this possibility. The data of Burger (1953) for S. vulgaris suggest this possibility. Although the effective difference between these two interpretations of the functional relationship between p and k is relatively trivial for Z. l. gambelii this may not necessarily be the case for other species. It is obvious that one way in which testicular maturation can be attained earlier in the year is with a lower value of q, or with a stronger curvilinear relationship between p and k in the lower tail of the curve. It is also obvious that when q is less than the shortest winter day, or, in the alternative interpretation of the relationship between p and k, when k has an appreciable value at the lowest winter values of p, the time of termination of the refractory period may become important with respect to the curve of testicular development. It seems possible that this could be applicable to certain non-migratory British species in which abortive fall and midwinter sexual activity has been noted (Marshall, 1949, 1952). An essential part of such a hypothesis would be a more marked relationship between k and the temperature coefficient (c).

The literature actually contains very little useful data on the minimum effective day-length (q). For S. vulgaris it appears to be less than 8.5 hours (Burger, 1949). A recalculation of the data of Bartholomew (1949, Fig. 15) suggests that q is about nine hours for P. domesticus. However, because, in another experiment his data (p. 444) contain two cases of at least some histologic development at 8-hour photoperiods, it is possible that the alternative interpretation of the relationship between p and k may hold. In considering the matter of the minimum effective day-length (q), it is necessary to bear in mind the possibility of the existence of an internal timer as Miller (1955) has suggested for Zonotrichia coronata and

Zonotrichia leucophrys nuttalli. The data of Benoit *et al.* (1955) suggest a similar possibility in ducks.

Another way in which the time of maturation of the testes may be affected is by the rate of testicular growth (k) once stimulatory day-lengths occur. As indicated in equation (7), a greater slope constant a will result in a more rapid development. From the data of Bartholomew (1949) for *P. domesticus* it has been possible to calculate a curve relating k to p. In this calculation it has been assumed that the rate of testicular growth under the influence of daily photoperiods of constant length is in accordance with the logarithmic curve expressed by equation (1). Values of k for several different photoperiods have been similarly calculated from data obtained for this species in our laboratory and from Vaugien (1952). These values are consistent with the curve derived from Bartholomew's data. The curve is similar to that of *Z. l. gambelii* (Fig. 3); however, the linear part is steeper, a being 0.013 compared to 0.009 and 0.008 for first-year and adult *Z. l. gambelii*. It appears, then, that the greater value of a for *P. domesticus* correlates well with the earlier testicular development of this species in nature. It should be observed that direct comparisons of a for different species are meaningful only when the differences between the logarithms of the resting and developed testes are very similar. This is essentially true for *Z. l. gambelii* and *P. domesticus*.

It should also be noted that a greater adjustment to the conditions of the developing season could be obtained with a greater sensitivity to environmental temperature as indicated in equation (3). As c becomes greater the time of maturation would fluctuate more as a function of environmental temperature. This would be particularly valuable to an early breeding, non-migratory species, but also of some value to species whose migratory route is confined to a relatively restricted range of temperate-zone latitude. As noted above, it would be very interesting to investigate the British species discussed by Marshall (1949, 1952) with respect to temperature sensitivity, the termination of the refractory period, and the functional relationship between p and k.

It is obvious that variations in the values of a, c, q (or the nature of the lower tail of the curve relating k to p), and the terminal dates of the refractory periods could produce a wide range of times at which testes mature. However, it must be re-emphasized that these arguments are derived almost exclusively by extrapolation from experiments on a single population of *Z. l. gambelii*. It would be of great interest to examine additional species similarly.

SUMMARY

1. The rate of testicular development in *Zonotrichia leucophrys gambelii* has been examined quantitatively as functions of day-length, light intensity, and environmental temperature.

2. From these laboratory-established relations a predicted curve for testicular growth under natural conditions was calculated and compared with data obtained from a natural population. The predicted curve indicates the attainment of 100-mg. combined testicular weight about ten days earlier than its occurrence in the natural population. Although this relatively small discrepancy may be reasonably explained on a statistical basis, it is not possible to rule out minor effects by environmental variables other than daily photoperiod and temperature.

3. The calculations, and the relatively close agreement with the observations of the natural population, emphasize quantitatively the overwhelming importance of the daily photoperiod as the primary timer in the testicular cycle for this population of *Zonotrichia leucophrys gambelii*. Other environmental factors, as they operate in the Snake River Canyon, appear to be responsible for fluctuations with a combined maximum possible magnitude of the order of ten days to two weeks.

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